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Mutual ornamentation, age, and reproductive performance in the European starling

Jan Komdeur,[a] Margot Oorebeek,[a] Thijs van Overveld,[a] and Innes C. Cuthill[b]
[a]Animal Ecology Group, Centre for Evolutionary and Ecological Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands, and [b]School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1 UG, UK

Ornamental traits expressed in both sexes are widespread among birds. Many studies have indicated that male ornaments develop through sexual selection. Female ornaments may be correlated effects of selection on males or have signaling functions in their own right. In the facultatively polygynous starling *Sturnus vulgaris*, both sexes possess iridescent throat feathers, which are actively displayed during courtship by males. This paper investigates the reproductive correlates of throat feather ornaments in both sexes. Bird-perceived hue and components of feather length covaried strongly, and a summary variable (the first principal component [PC1]) was extracted using Principal component analysis. Sex and age-related differences were found for PC1. Positive assortative mating was found with respect to age and PC1. However, the relative influences of ornamentation and age on breeding variables were hard to separate, so effects may be related to other age-related variables. This provides a cautionary note for studies of ornamentation where age is unknown. However, we argue that throat feathers in starlings may signal age and age-related quality measures in both sexes. Older females with higher PC1 scores bred earlier and laid larger clutches with higher hatching success; older males with higher PC1 scores had higher chances of becoming polygynous and attracting high reproductive quality females. PC1 showed no relationship with parental care in either sex. Direct reproductive benefits for males and indirect genetic benefits for either sex may drive mate choice based on these age-related characters. However, only experimental manipulation can determine whether ornamentation signals quality variation within age classes. *Key words:* avian color vision, mutual sexual selection, ornamentation, plumage coloration, reproductive performance. *[Behav Ecol 16:805–817 (2005)]*

Sexual selection theory has proved extremely successful in explaining male ornaments, such as elaborate vocal and visual displays (reviewed by Andersson, 1994). Several studies have provided conclusive evidence that females can assess the variation in male quality if males in better condition express more elaborate displays and that females prefer more conspicuously ornamented males (reviewed by Hill and Montgomerie, 1994; Ryan, 1997). Females paired with attractive partners may thus gain direct benefits, such as territorial resources and parental care, or indirect benefits, such as more viable offspring, as suggested by the good-genes process, or more attractive offspring, as suggested by the Fisher process (reviewed by Andersson, 1994). The size and/or intensity of expression of these ornaments may depend on condition, age, or both (Andersson, 1994). In several species females also show some expression of the same ornaments as males. It has been suggested that ornaments selected for in males are also expressed in females simply because they carry the genes for these traits and sex limitation is incomplete (Cuervo et al., 1996; Lande, 1980, 1987; Lande and Arnold, 1985; Muma and Weatherhead, 1989). On this view, female ornaments are a by-product of sexual selection in males and selectively neutral or deleterious in females. The latter is likely because most models of sexual selection assume a cost to the production of the ornamental trait (Johnstone, 1995). For this reason, unless females benefit from expressing a costly ornament, we would expect selection for sex limitation of the ornament to males (e.g., Rice and Holland, 1997), and thus genetic correlations are unlikely to provide a complete explanation of female ornamentation. Indeed, in birds at least, empirical evidence for this explanation is rare (e.g., Roulin et al., 2001), and the phylogenetic evidence suggests that evolutionary changes between sexual monomorphism and dimorphism are relatively unconstrained (Amundsen, 2000a,b). The alternative explanation for similar ornamentation in males and females is that sexual selection acts on females as well as on males. Female ornaments may signal social dominance in contests over limited resources, such as territories or mates (Irwin, 1994; West-Eberhard, 1983), or they may indicate reproductive, parental, or genetic quality and hence are preferred by choosy males (Amundsen et al., 1997; Johnsen et al., 1996; Jones and Montgomerie, 1992; Linville et al., 1998; Potti and Merino, 1996). Thus, similar preferences in both sexes can explain ornamentation of both sexes in some bird species (Jones and Hunter, 1993, 1999; Hunt et al., 1999). Mutual sexual preference and mutual ornamentation are expected to occur in species where fitness in both sexes is strongly related to mate quality rather than quantity. The standard arguments for male ornamentation and female choice (Andersson, 1994) predict female ornamentation and male choice where, for example, males provide a substantial amount of parental care to the offspring (Johnstone et al., 1996; Kokko and Johnstone, 2002; Trivers, 1972) or where male reproductive success is limited by female reproductive or parenting ability (Grafen, 1990; Heywood, 1989; Hoelzer, 1989). Selection for mutual signaling of condition is expected in species where pair formation occurs every breeding season (offering considerable potential for exercising choice) and where both sexes vary substantially in quality and make large contributions to rearing the offspring (Johnstone et al., 1996; Trivers, 1972).

The facultatively polygynous European starling (*Sturnus vulgaris*) is a semicolonially breeding, hole-nesting passerine. In our population most starlings (95%) arrive at the breeding ground within a short interval (4–12 days) in March, 2 weeks before nest building. The arrival date is independent of the bird's age and sex, and the time between arrival and pair

Address correspondence to I.C. Cuthilli. E-mail: i.cuthill@bristol.ac.uk.
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formation is 5–15 days (Brouwer and Komdeur, 2004). Pair formation occurs every season, and in monogamous breeding pairs both members contribute substantially to both incubation and feeding of the young (Komdeur et al., 2002; Pinxten and Eens, 1994; Pinxten et al., 1993; Sandell et al., 1996; Smith et al., 1995; Wright and Cuthill, 1992). Reduced male parental contributions to either incubation or feeding result in lower overall care (the female does not compensate fully for reduced male investment; Komdeur et al., 2002; Pinxten et al., 1993; Wright and Cuthill, 1989) and reduce brood value through increased hatching and fledging failure or lower fledging mass (Komdeur et al., 2002). During the breeding season both sexes possess iridescent throat feathers (Feare, 1984), which vary in color depending on the angle of viewing (Cuthill et al., 1999). Males have longer throat feathers but, although sexual dimorphism in throat plumage becomes more pronounced in the breeding season, differences in coloration between the sexes remain subtle to human eyes (Feare, 1984). Male starlings actively display their throat feathers to females during courtship (Eens et al., 1990; Feare, 1984), and the sexual dimorphism in size and iridescence of these feathers indicates that they are likely to be involved in sexual selection (Cuthill et al., 1999). Laboratory mate-choice experiments have shown that there are differences in the reflectance spectra of the throat feathers of preferred and nonpreferred males (Bennett et al., 1997). Preferred males have relatively high reflectance at both 400–500 nm and 600–700 nm (so appear purple to humans), while nonpreferred males have feathers with weaker overall reflectance and maxima both below 400 nm (near-ultraviolet [UV]) and from 500 to 600 nm (so appear green to humans). Based on what is known about starling visual pigments (Hart et al., 1998) and the fact that the removal of the UV component affects choice (Bennett et al., 1997; Maddocks et al., 2002), we can surmise that, to a female starling, preferred males have relatively saturated purplish throat feathers, while nonpreferred males have unsaturated UV-green throat feathers. However, it is unknown whether the preferences observed in the laboratory translate to the field and whether natural mate choice is influenced by coloration or superseded by other display traits such as song. If coloration is important in the field, we do not know why such males would be preferred. We also lack any information on whether males prefer similar or the opposite plumage features in females.

In the paper we have three aims. First, we aim to document any relation between the variation in throat feather characteristics (e.g., color and lengths of feathers) among individuals in relation to sex, age, and body size. Second, we test for a relation between ornamentation and social pair formation by comparing the characteristics of throat feathers between members of social pairs (cf., the assortative pairing by UV coloration in blue tits, *Parus caeruleus*; Andersson et al., 1998). Third, we examine whether throat feather characteristics predict parental care or reproductive performance in either sex. Until now there have been only a few studies on the relation between ornamentation and reproductive success in species where both males and females express the same ornament (Cuervo et al., 1996; Hill, 1993; Muma and Weatherhead, 1989), but none of these studies have concerned iridescent ornamentation. Furthermore, this is the first study to investigate the relation between mutual ornamentation and reproductive success in a facultatively polygynous species.

METHODS

Study population and data collection

Starlings were studied at a colony of 112 nest-boxes at Vosbergen, near Groningen (The Netherlands) during the breeding season (early February to late June) in the 3 years from 2000 to 2002. The colony consisted of uniform nest-boxes, situated approximately 6 m apart at a height of 2.5 m. The population was single brooded. During the early nestling stage, male and female starlings were caught with nest-box traps. During capture, birds that were not already ringed were individually color banded and weighed to the nearest gram using a 100-g Pesola balance. Birds were sexed based on bill-base coloration (pink in females, blue in males), the female-specific eye-ring, and plumage characteristics of breast and abdomen (Feare, 1984). Molecular sexing (Griffiths et al., 1998) of 51 birds in the study and an independent validation using another 100 birds (Smith EL, Greenwood VJ, Cuthill, Goldsmith AR, and Griffiths R, unpublished data) were 100% consistent with sexing based on morphological features. Tarsus and wing lengths were measured twice to the nearest 0.1 mm using vernier calipers and to the nearest 1 mm using a ruler, respectively. From each bird 8–10 feathers were randomly collected in a standard region of the throat. Removal of feathers was performed by pulling the feathers near the base with forceps. When done swiftly by a skilled bird handler, the discomfort to the bird appeared brief. Unfortunately, removal by cutting would not have allowed measurement of total feather length. Thereafter, feathers were handled with forceps. Feathers were individually housed in plastic envelopes, which were given codes so that feather length measurements and reflectance spectrophotometry could be performed blind to the sexual and individual identity of the bird from which the feather had come.

We observed all breeding pairs over the full breeding cycle (2000, 33 pairs; 2001, 31 pairs; 2002, 25 pairs) to quantify reproductive behavior and male mating status (monogamous or polygynous). Because eggs are usually laid before 1100 h (Meijer, 1992; Pinxten and Eens, 1998), the nests were checked daily between 1100 and 1230 h for the presence of eggs and start of incubation (determined by feeling the egg temperature). All nests with eggs were observed on day 5 or 6 of incubation (incubation day 0: the first day the eggs were assessed as warm) for 90 continuous min between 1000 and 1300 h. Telescopes, placed 50–60 m away from the focal box, were used to allow identification of individuals as they arrived at and departed from their nest. For each sex, we measured incubation attendance as the proportion of time spent in the nest-box. From day 11 of incubation each clutch was checked daily for the presence of hatched and unhatched eggs. All nests with broods were watched for 90–120 continuous minutes between 1000 and 1300 h on day 12 or 13 after the first young in that nest hatched, following the same protocol as above. Birds that were not yet color banded during the incubation watch were distinguished by bill and plumage characteristics as described above. We are confident that the unringed birds observed during incubation and ringed during the nestling stage were the same individuals because the already banded birds remained faithful to their nest-box from incubation to provisioning (Brouwer and Komdeur, 2004). For each sex, we measured the food provisioning in terms of visits per hour. When the nestlings were 18 days old (approximately 3 days before fledging), we measured the mass to the nearest 1 g using a 100-g Pesola balance and tarsus to the nearest 0.1 mm using vernier calipers.

Feather measurements

Measurements of length (by M.O. and T.v.O.) and spectral reflectance (by I.C.C.) were taken from each throat feather. The following length measures were quantified (to the nearest 0.1 mm, using a binocular microscope and calipers; Figure 1): tip length (the length of the dark portion of the feather), gray length (the length of the gray portion of

Figure 1
Measurements taken from two male starling throat feathers.

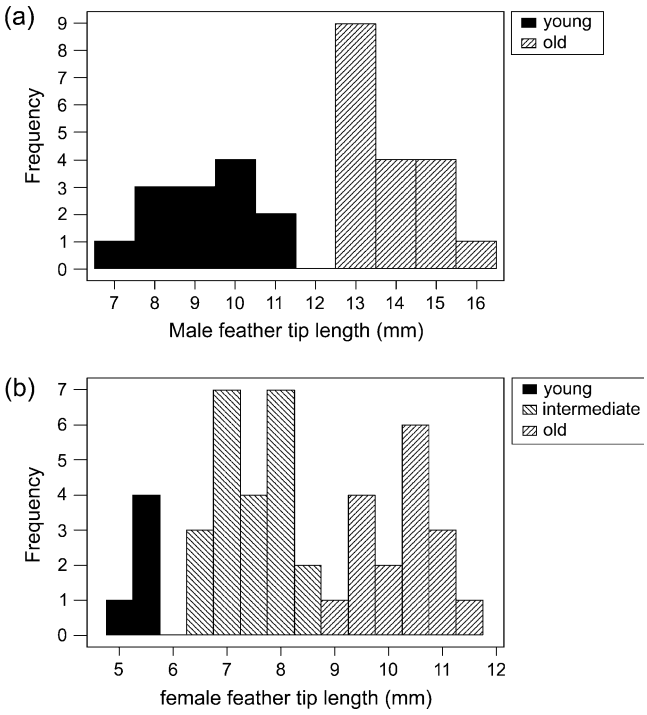

Figure 2
Feather tip lengths of (a) male and (b) female starlings, aged according to Svensson (1992).

the feather), total feather length (tip length and gray length), and iridescence length (the length of the iridescent portion of the feather). Length of the white spots, present on the tips of feathers when freshly molted, were not included in total length as in all birds these spots had worn off. The length measures of each feather were taken twice. The mean tip length was used to assign birds into age classes according to Svensson (1992). Male and female starlings in their first breeding season (hereafter termed "young birds") have smaller tip lengths than males and females that are at least 3 years of age (hereafter termed "old birds;" males: range of tip lengths, young 7.0–11.0 mm and old 12.0–15.5 mm; females: range of tip lengths, young <6.0 mm and old 9.0–12.0 mm). In our sample, male tip lengths were clearly bimodal (Figure 2a), with no intermediates between 11.0 and 12.0 mm. Females, on the other hand, had a trimodal distribution (Figure 2b), with tip lengths between 6.0 and 9.0 mm forming a discrete class between those that the criteria of Svensson (1992) designate as "young" and "old" (we term these "intermediate" females). The trimodal female, but bimodal male, tip length distribution accords with the fact that while some females breed in the year after fledging, males do not start to breed until the next year (Feare, 1984; Komdeur J, unpublished data). Thus young breeding males are a year older than young females, but we retain the nomenclature of Svensson for consistency with previous literature. We are confident about this method of ageing because recaptured wild birds of known age had tip lengths within the given range, and repeated annual measurements of birds caught as fledglings, and held in captivity, fitted the above ageing criteria without exception (Komdeur and Cuthill, unpublished and independent data).

The general protocol for spectrophotometry was exactly as in Cuthill et al. (1999). We used a Zeiss MC 500 UV-IR spectrophotometer, with continuous dark current adjustment. Feathers were mounted on black cloth to eliminate stray reflection from the background and then illuminated with a Zeiss CLX 500 xenon lamp from the proximal end, as would usually be the case for downward-pointing throat feathers under most natural lighting conditions. Illuminating and measuring angles were equal and opposite, at 45° to normal, with the feather parallel to the light beam. The geometry was chosen as the amount of the reflected light is high and the sex differences are clear (Cuthill et al., 1999). Light was focused on approximately 2-mm-diam area using a quartz lens and UV-transmitting fiber optics and light collected by a similarly focused lens. The measurements were expressed relative to a Spectralon™ 99% white reflection standard, in 1-nm steps from 300 to 700 nm. White reference measurements were taken immediately before measuring each feather, in order to minimize any error associated with drift of the light source or sensor. Each feather was measured five times, each measurement was from a randomly chosen area within the iridescent part, and the feather was removed from the apparatus and repositioned each time.

From the reflectance measurements we calculated the photon catches of the starling's four single-cone types when viewing that spectrum under a standard daylight illuminant (D65; Wyszecki and Stiles, 1982). The color space model is the one described in Maddocks et al. (2001), using the data for starling visual pigments, oil droplets, and optical media transmission in Hart et al. (1998). From these cone photon catch data, we calculated three derived measures that were predicted to be relevant in starling mate choice. Bennett et al. (1997), in laboratory mate-choice experiments, found that preferred males had throat feathers with (1) reflectance spectra peaking in the short wavebands (SW) and long wavebands (LW) rather than the UV and medium wavebands (MW), (2) spectra with more sharply defined peaks, and (3) spectra with higher mean reflectance. Based on well-established relationships between spectral shape and perceived color (Endler, 1990), Bennett et al. (1997) concluded that preferred male starlings would have throat feathers that were (1) more purple (and less UV-green), (2) more saturated (higher chroma), and (3) brighter. Our derived color indices were designed to represent these three qualities: "hue index" is the ratio of SW + LW cone catches to the UV + MW catches. Whilst this is only one possible hue dimension in bird color space (Cuthill et al., 2000), we have independent evidence that it should matter

to starlings: not only do the results of Bennett et al. (1997) suggest that male variation lies along this dimension, the spectra in Cuthill et al. (1999) suggest that male-female color differences do too. The "chromatic index" is calculated from the representation of each spectrum in a tetrahedral color space (according to Burkhardt, 1989; see also Maddocks et al., 2001). The apices of such a color space represent spectra that stimulate only one cone type exclusively (100% UV, SW, MW, or LW cone catches) and the center of the tetrahedron is where all cones are stimulated equally (25%, 25%, 25%, 25%). Thus, the center represents the "achromatic locus" of white through grays to black, and the apices represent the pure "bird primary colors." Our chromatic index is the Euclidian distance from the center of the tetrahedron to the point representing the spectrum in question. Our final color measure is the "brightness index," which is the simple sum of all four cone catches. We make no claims that any of these measures are linearly related to perceived qualities of color or even that starlings experience such qualities, but they are a logical step closer to the quantification of starling-perceived colors in the absence of psychophysical data. For each feather variable, the mean, across replicates and feathers, was calculated for each individual, and this value was used in subsequent analyses.

Data analyses

Each pair produced only one clutch per year. Observations involved different pairs each year; for four birds (three females, one male) that bred in more than 1 year, to avoid pseudoreplication we used only one season's data (the season for which we had complete data on both pair members). With the exception of total fledging output, where fledgling numbers across both nests were pooled, analyses for polygynous males were restricted to the primary female and her clutch. This is because it is she who was attracted and laid first, and it is to her nest that polygynous males directed care (see also Pinxten and Eens, 1994). We did not expect any difference between the mates of monogamous males and the primary females of polygynous males (Pinxten and Eens, 1990) but tested for this directly and included "mating status" in analyses where it could be a possible confounding factor. Intraspecific brood parasitism (as assessed by the presence in a nest of two or more new eggs in 1 day; Yom-Tov, 1980) occurred only once in our population, and this nest was excluded from further analysis because two females were attending the nest simultaneously. For each pair, the laying date of the first egg was related to the date when the first egg in the colony was laid in that year (laying date 1). As an estimate of body condition for 18-day-old nestlings and adults, we used body mass and not the regression residuals derived from the equation of mass versus tarsus because tarsus was not correlated with mass (Brouwer and Komdeur, 2004; see discussion in Green, 2001). For nestlings, the mean nestling mass per brood was used in analyses.

Of the 89 breeding pairs that produced a clutch, 49 females and 32 males were caught and measured. Of 32 monogamous pairs, the female (11), the male (7), or both breeding birds (14) were measured. Of the 32 males caught, 21 were monogamous and 9 were polygynous (attending two nests). Of the polygynous males caught, the primary female (6) or both females, the primary, and the secondary female (3) were measured. We were unable to determine the mating status of two captured males accurately in 2002 because of the occurrence of nest desertions between egg laying and the onset of observations. For 12 females we were unable to determine the mating status of their mates. For simplicity, we term the measured throat feather characteristics "ornamental traits" and tarsus and wing lengths "nonornamental traits." As an estimate of the measurement error, we calculated the repeatabilities of measurements for the tarsus, wing, and each feather (tarsus, wing, and measures of feather lengths were measured twice and spectra five times). The repeatability (r_I) of measures was derived from the intraclass correlated coefficient (Zar, 1999) calculated, in the case of feather measurements, from a nested ANOVA (measurement within feather and feather within bird). The measurements of all traits were significantly repeatable (total feather length: $r_I = .96$, $F_{80,324} = 175.99$, $p < .001$; tip length: $r_I = .96$, $F_{80,324} = 43.60$, $p < .001$; gray length: $r_I = .91$, $F_{80,324} = 20.91$, $p < .001$; iridescence length: $r_I = .98$, $F_{80,324} = 92.28$, $p < .001$; hue index: $r_I = .50$, $F_{311,1568} = 6.08$, $p < .001$; chroma index: $r_I = .48$, $F_{311,1568} = 5.55$, $p < .001$; brightness index: $r_I = .93$, $F_{311,1568} = 68.01$, $p < .001$; tarsus length: $r_I = .52$, $F_{80,324} = 3.19$, $p = .003$; wing length: $r_I = .74$, $F_{80,324} = 6.66$, $p < .001$). As an estimate of the reliability of our feather sampling technique, we calculated the repeatabilities of measurements for each individual (as several feathers were sampled from each bird). The feather sampling technique is representative because the measurements of all traits from different feathers of 81 individuals were highly repeatable (total feather length: $r_I = .96$, $F_{80,324} = 50.95$, $p < .001$; tip length: $r_I = .96$, $F_{80,324} = 45.85$, $p < .001$; gray length: $r_I = .85$, $F_{80,324} = 12.01$, $p < .001$; iridescence length: $r_I = .96$, $F_{80,324} = 55.66$, $p < .001$; hue index: $r_I = .74$, $F_{80,311} = 14.48$, $p < .001$; chroma index: $r_I = .28$, $F_{80,311} = 2.87$, $p < .001$; brightness index: $r_I = .61$, $F_{80,311} = 8.58$, $p < .001$).

We assessed age-related differences in throat feather measurements other than tip length, the latter being the trait used to age the birds (young or old birds, see above). In order to obtain normality of residuals, proportions of time spent incubating were square-root transformed (this was more effective than arcsine transformations) and the laying date was logged (base 10). The provisioning rate could not be normalized, so we used Kendall's rank-based τ statistic for both simple and partial correlations (Siegel and Castellan, 1988). Effects on clutch size and number of fledglings were analyzed using generalized linear models (GLM) with Poisson error and the scale parameter set to the square root of the deviance divided by the degrees of freedom to account for underdispersion (PROC GENMOD; SAS Institute, 1999). Effects on relative hatching and fledging success were analyzed with similar models but with clutch size as a covariate for the relative hatchling analysis and hatchling number as a covariate for the relative fledging success analysis. Principal component analysis (PCA) was used to investigate the covariance between ornamental traits and to reduce the number of dependent variables describing "ornamentation." Tip length was entered as a variable into the PCA, even though it was used as the ageing criterion because tip length may carry information about, for example, an individual's quality and may be used as a cue in mate assessment. A PCA with tip length included does not result in circularity for two reasons. (1) If a PCA on the feather variables is conducted, but excluding tip length, the correlation between the new first principal component [PC1] (excluding tip length) and the old PC1 (including tip length) is 0.985, and the correlation between the new second principal component [PC2] and the old PC2 is 0.988. This means that the same results would be obtained even if one were to avoid the potential circularity of using tip length as both an ageing variable and in the PCA. (2) Tip length shows discrete variation between ages whilst there is still continuous variation within age categories. Feather length was not entered into the PCA because it is the simple sum of the tip and gray portion of the feathers (Figure 1). We quote unstandardized slopes (b) for regressions and GLMs, means are expressed with standard errors (SE), probability values are two tailed, and the null hypothesis was rejected at a tablewide

Table 1
Correlations between ornament measures and results of PCA

	Feather	Irid	Tip	Gray	Hue	Chroma	Bright	PC1	PC2
Feather length	1.000							—	—
Iridescence length	0.829	1.000						.914	−.202
Tip length	0.909	0.926	1.000					.931	−.150
Gray length	0.717	0.307	0.363	1.000				.483	−.130
Hue index	0.659	0.761	0.731	0.251	1.000			.801	−.358
Chroma index	0.211	0.245	0.273	0.016	0.085	1.000		.403	.834
Brightness index	0.539	0.451	0.508	0.359	0.360	.492	1.000	.695	.486

Values below the diagonal of the matrix are pairwise Pearson correlation coefficients ($n = 77$, any $r > .224$ has $p < .05$ uncorrected, or $r > .355$ Bonferroni corrected for tablewide $\alpha = 0.05$). The two right-hand columns are the correlations between the first two principal component scores and the variables from which they were extracted (feather length, being the sum of tip and gray length, was not entered into the PCA).

$p < .05$ (i.e., per family of tests; Chandler, 1995) using the sequential Bonferroni method (Rice, 1989).

RESULTS

Covariance of ornamental traits

All measured components of feather length and spectral reflection were positively correlated (Table 1), although the relationships between the chroma index and the other variables were generally weak. The first two components derived from PCA of the correlation matrix explained 73% of the variation in the raw variables, and only these components had eigenvalues greater than 1. PC1 (54% of the variance) was highly correlated with all components of feather length, particularly the iridescent portion, and also the hue. PC2 (19%) was largely related to the chroma index. PC1 and PC2 were hereafter used as proxy variables for feather length and color measurements. Interestingly, the correlation matrices and results of PCA were very similar when males and females were analyzed separately (results not shown, but illustrated by Figure 3).

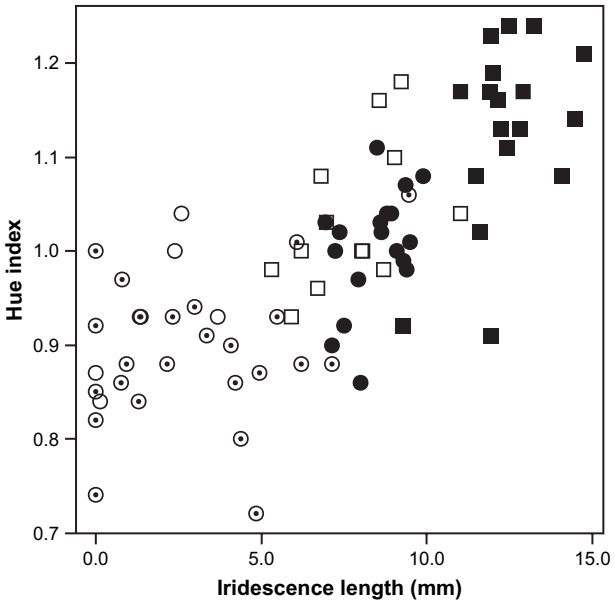

Figure 3
Covariation between hue index and iridescence length of starling throat feathers. Solid squares, old males; clear squares, young males; solid circles, old females; dot circles, intermediate females; clear circles, young females.

Ornamental and nonornamental traits in relation to age and sex

Sex and age differences were found in ornamental traits, but only sex differences were found in nonornamental traits (Table 2). PC1 was the component of ornamentation that varied; there were no sex or age differences in PC2. Males had significantly longer and more purple (high hue index) throat feathers than females. The sex differences were mirrored in the age differences: PC1 was significantly larger in older birds (Table 2). This is not a simple by-product of tip length being used as the ageing criterion: if you do a new PCA on the feather variables but omit tip length, then the correlation between the new PC1 and that presented here is 0.985 and the correlation between the new PC2 and the PC2 presented here is 0.988.

There were no sex by age interactions; the marginal effect for iridescence length ($p = .024$, ns after sequential Bonferroni correction) results from the age difference tending to be greater in females (Table 2). The length and color of old female throat feathers was similar to that of young males (Figure 3; Table 2); young females had distinctly UV-green feathers (hue index <1). Ornamental traits were quite variable with coefficients of variation ranging from 6.3% to 92.4% (Table 2). However, the variability of these traits was very similar for males and females, old and young birds (Table 2). CVs of ornamental traits were significantly higher than CVs of nonornamental characters (tarsus and wing lengths with CVs ranging from 1.5% to 4.1%; Table 2; *F* tests, following Lande, 1977, for all pairwise comparisons of ornamental versus nonornamental traits, for all sex-age classes, $p < .05$ for all tests).

Ornamentation versus morphology

Tarsus length, wing length, and body mass did not vary with ornamentation in either males or females (males: PC1-tarsus, $r_{29} = .100$, PC2-tarsus, $r_{29} = .067$; PC1-wing, $r_{29} = .248$, PC2-wing, $r_{29} = .171$; PC1-mass, $r_{29} = .305$, PC2-mass, $r_{29} = .026$; females: PC1-tarsus, $r_{43} = .098$, PC2-tarsus, $r_{43} = .237$; PC1-wing, $r_{43} = .114$, PC2-wing, $r_{43} = .043$; PC1-mass, $r_{43} = .097$, PC2-mass, $r_{43} = .176$; all $p > .10$ uncorrected for multiple

Table 2
The influence of age and sex on ornamental and nonornamental traits of European starlings

	Old males ($n = 18$)			Old females ($n = 16$)			ANOVA results: F ratio (p value)[a]		
Traits	Mean	SE	CV	Mean	SE	CV	Age	Sex	Age × sex
Tarsus length (mm)	30.5	0.21	2.9	29.3	0.23	3.7	14.50 (<.001)[b]	0.24 (.630)	0.05 (.820)
Wing length (mm)	133.1	0.50	1.6	129.4	0.46	1.5	36.98 (<.001)[b]	1.89 (.176)	0.29 (.592)
Total feather length (mm)	22.0	0.49	9.4	17.5	0.38	10.2	63.35 (<.001)[b]	88.56 (<.001)[b]	0.24 (.625)
Iridescence length (mm)	12.4	0.29	9.9	8.5	0.21	10.8	155.45 (<.001)[b]	195.83 (<.001)[b]	5.47 (.024)
Gray length (mm)	8.1	0.49	25.3	7.2	0.34	21.2	3.62 (.063)	3.70 (.060)	0.12 (.735)
Hue index	1.13	0.02	8.6	1.01	0.01	6.3	19.87 (<.001)[b]	9.39 (.004)[b]	0.41 (.524)
Chroma index	0.05	0.01	36.7	0.04	0.00	54.6	2.16 (.148)	0.51 (.480)	0.90 (.348)
Brightness index	0.91	0.07	35.3	0.76	0.06	31.6	7.03 (.011)	14.87 (<.001)[b]	1.35 (.251)
PC1	1.35	0.12		0.17	0.10		69.68 (<.001)[b]	81.55 (<.001)[b]	0.37 (.546)
PC2	−0.21	0.24		−0.24	0.22		0.04 (.851)	0.06 (.812)	0.12 (.728)
				Intermediate females ($n = 24$)					
Tarsus length (mm)				29.7	0.25	4.1			
Wing length (mm)				129.8	0.48	1.8			
Total feather length (mm)				14.3	0.33	11.3			
Iridescence length (mm)				3.0	0.55	90.4			
Gray length (mm)				6.6	0.25	18.6			
Hue index				0.89	0.02	8.8			
Chroma index				0.04	0.00	43.6			
Brightness index				0.63	0.05	40.8			
PC1				−0.84	0.09				
PC2				0.43	0.21				
	Young males ($n = 13$)			Young females ($n = 5$)					
Tarsus length (mm)	30.3	0.13	1.6	29.2	0.51	3.9			
Wing length (mm)	132.5	0.64	1.7	128.0	1.30	2.3			
Total feather length (mm)	16.6	0.54	11.7	11.4	0.88	17.3			
Iridescence length (mm)	7.73	0.44	20.6	1.8	0.73	92.4			
Gray length (mm)	7.3	0.40	19.7	6.0	0.83	30.7			
Hue index	1.03	0.02	7.4	0.94	0.04	9.0			
Chroma index	0.04	0.01	49.8	0.04	0.01	47.7			
Brightness index	0.68	0.07	39.4	0.35	0.09	54.9			
PC1	0.04	0.15		−1.35	0.17				
PC2	−0.21	0.26		−.04	0.43				

[a] For all tests df = 1,48.

[b] Significant differences at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis. ANOVAs do not include intermediate females, only definite old and young birds. Coefficients of variation (CVs) are not quoted for PCs as the scale of measurement is centered on 0.

testing). Controlling for age in multiple regressions did not alter the relationships.

Ornamentation and pairing

Before looking for evidence of deviations from random mating in relation to starling ornaments, we used analysis of covariance to check for differences between years in the relationships between male and female ornaments within pairs. None of these relationships differed significantly between years (ANCOVAs, $p > .10$ for each year-by-trait interaction), so pairs from 2000, 2001, and 2002 were pooled for further analyses. There was no assortative pairing in relation to male and female tarsus length or body mass, although a correlation between wing lengths was evident (Table 3). Strong assortative pairing by ornamentation (as measured by PC1, but not PC2; Figure 4; Table 3) reflected high within-pair correlations in iridescence length ($r_{18} = .834$, $p < .001$), feather length ($r_{18} = .682$, $p < .001$), tip length ($r_{18} = .774$, $p < .001$), and hue index ($r_{18} = .651$, $p = .002$). However, there was also assortative pairing by age (old males with old/young-or-intermediate females = 7/3; young males with old/young-or-intermediate females 0/10; Fisher's Exact test: $p = .003$). In order to try to separate associations due to the traits per se and due to age, we performed two further sets of analyses. We tested for assortative pairing on morphology independent of age by regressing the male trait on male age, the female trait on female age, and then correlating the residuals from the two analyses (reducing the degrees of freedom by 2 to allow for the fact that the residuals are estimated from fitted slopes in each case). No ornamental or nonornamental traits were correlated after controlling for age. Before concluding that there is no assortative pairing by ornamentation other than that accounted for by age, it is also important to consider the reverse possibility, so we tested for age associations independent of assortative pairing with respect to each trait. We did this by correlating the residuals of a binary logistic regression of female age on the female trait and the analogous residuals from logistic regression of male age on the male trait. The only trait that abolished the observed age-assortative pairing, when controlled for statistically, was PC1 (Table 3). In summary, age and ornamentation, as measured by PC1, are too highly correlated with each other to distinguish their separate contributions to assortative pairing.

Polygynous males were more ornamented than monogamous males, as measured by PC1 ($t_{25} = 3.64$, $p = .001$) but not PC2 ($t_{25} = 1.63$, $p = .116$). However, polygynous males were also more likely to be old males (0/12 younger males were polygynous, while 8/17 older males were polygynous ($p = .009$ by Fisher's Exact test). The difference in PC1 between polygynous and monogamous males disappeared after

Table 3
Correlations between male and female parents in nonornamental and ornamental traits

Variable	Raw		Age-controlled		Trait-controlled	
	r	*p*	*r*	*p*	*r*	*p*
Tarsus	.036	.860	−.144	.544	.764	<.001[a]
Wing	.529	.005[a]	.325	.161	.713	<.001[a]
Mass	.263	.195	.145	.543	.760	<.001[a]
Ornament PC1	.754	<.001[a]	.193	.416	.311	.181
Ornament PC2	.224	.304	.298	.202	.710	<.001[a]

[a] Significant differences at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis.

For polygynous males, only the primary female is included. "Raw" correlations (df = 18) are between the measured variables for pair members. "Age-controlled" correlations (df = 16) are between the residuals of a regression of the female values on female age and the residuals of a regression of the male value on the male age. "Trait-controlled" correlations (df = 16) test for associations between the ages of pair members, having controlled for the association in the trait in question. They are correlations between the residuals of a binary logistic regression of female age on the female trait and the analogous residuals from logistic regression of male age on the male trait.

controlling for age via multiple regression (age: $t_{26} = 5.16$, $p < .001$; mating status: $t_{26} = 0.57$, $p = .576$).

The mates of monogamous males and the primary females of polygynous males did not differ in size (tarsus: $t_{22} = 2.05$, $p = .053$; wing: $t_{22} = 1.72$, $p = .099$; mass: $t_{22} = 0.67$, $p = .509$) or ornamentation (PC1: $t_{16} = 1.81$, $p = .090$; PC2: $t_{16} = 1.93$, $p = .072$), but the nonsignificant trends were for primary polygynous females to be larger and more ornamented (higher PC1).

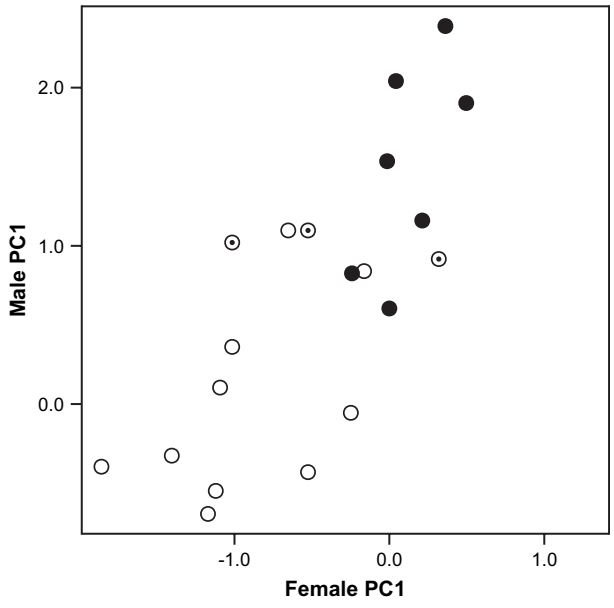

Figure 4
Male PC1 ornamentation score in relation to that of their mates. Open circles, young males paired to young females; dot circles, old males with young females; solid circles, old males with old females.

Table 4
Relationships between clutch size and male and female nonornamental and ornamental traits

Parameter	Simple effect			Age controlled		
	Estimate	χ^2	*p*	Estimate	χ^2	*p*
Males						
Tarsus	0.0096	0.03	.852	−0.0187	0.21	.646
Wing	0.0211	1.59	.207	0.0124	0.79	.375
Mass	−0.0007	0.01	.926	−0.0119	3.61	.057
Ornament PC1	0.1317	11.82	<.001[a]	0.0519	0.78	.376[b]
Ornament PC2	0.0019	0.00	.961	−0.0019	0.00	.953
Age	0.2440	15.05	<.00[a]	—	—	
Females						
Tarsus	−0.0428	3.10	.078	−0.0381	3.12	.077
Wing	0.0050	0.16	.688	−0.0029	0.07	.798
Mass	−0.0035	0.15	.697	−0.0021	0.07	.791
Ornament PC1	0.1539	21.07	<.001[a]	0.1176	5.09	.024[b]
Ornament PC2	0.0142	0.25	.6183	0.0043	0.03	.868
Age	0.3040	14.40	<.001[a]	—	—	—

[a] Significant differences at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis.

[b] Indicates that if the term is forced into the model before age, then age also ceases to have a significant effect.

$n = 28$ for males, 46 for females. For polygynous males, only the primary female is included. Analysis is by GLMs with Poisson error and the scale parameter adjusted to account for underdispersion. χ^2 Tests, with 1 df, are based on the change in log likelihoods as a result of adding the factor in question. The left-hand columns of tests are based on the change compared to a model with only a constant term. The right-hand columns of tests are the effect of the factor after controlling for age by forcing it into the model first.

Ornamentation, reproductive success, and parental care

Clutch size was strongly positively related to both male and female ornamentation (as measured by PC1, but not PC2; Table 4); males and females with longer feathers, higher lengths of iridescence, gray and tip, and a higher hue index had larger clutches. However, clutch size was also strongly related to both male and female age, and after controlling for age, PC1 ornamentation and clutch size were no longer significantly related (Table 4; although the relationship with female PC1 was marginal at $p = .024$, ns after Bonferroni correction). That said, if PC1 is entered into the GLM before age, then age ceases to be significant in both males and females (Table 4). The conclusion is that age and the PC1 measure of ornamentation are so tightly correlated that it is impossible to separate their influences on clutch size statistically. However, the relative influence of the male versus female pair member on clutch size can be separated. Male PC1 score ceases to be significantly related to clutch size when the PC1 score of his mate is controlled for (females: parameter estimate = 0.274, $\chi^2 = 11.71$, $p < .001$; males: estimate = −.016, $\chi^2 = .08$, $p = .774$). Likewise a GLM of clutch size with male and female age removes the influence of male age (females: estimate = 0.334, $\chi^2 = 3.86$, $p = .049$; males: estimate = 0.115, $\chi^2 = 1.15$, $p = .284$). Therefore, it is the relationship between female age/ornamentation and clutch size that appears to be the direct one. The primary females of polygynous males laid larger clutches than monogamously mated females ($\chi^2 = 6.28$, $p = .012$), but on entering both mating status and female age into the model, the differences between primary polygynous

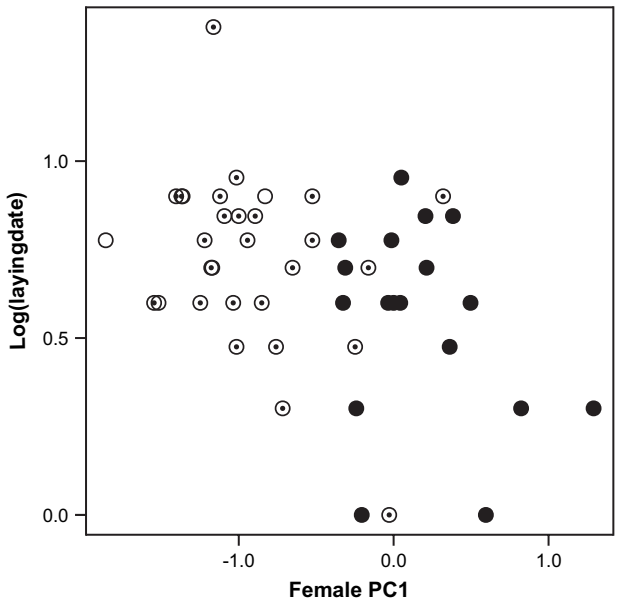

Figure 5
Relative laying date ($\log_{10}$ transformed) as a function of female PC1 ornamentation score. Open circles, young females; dot circles, intermediate females; solid circles, old females.

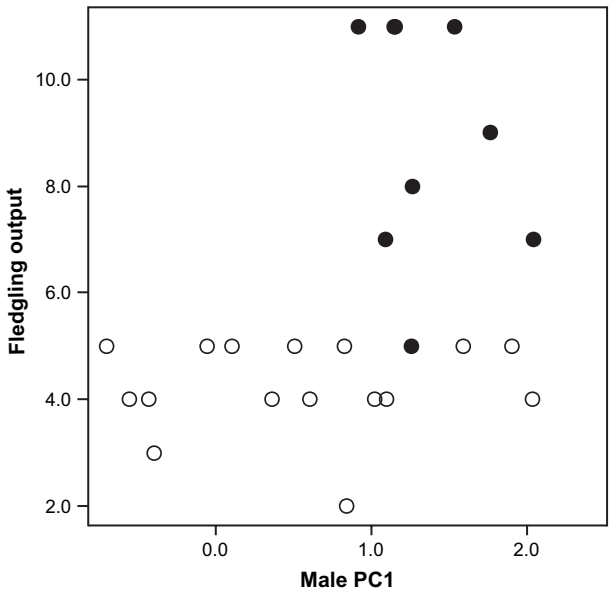

Figure 6
Total fledgling output against male PC1 (solid circles, polygynous males; clear circle, monogamous males).

and monogamous females disappeared (age: $\chi^2 = 11.09$, $p < .001$; mating status: $\chi^2 = 1.96$, $p = .162$). Likewise, entering both mating status and female PC1 into a model resulted in the differences between primary polygynous and monogamous females disappearing (age: $\chi^2 = 7.80$, $p = .005$; mating status: $\chi^2 = 0.70$, $p = .404$).

More ornamented (high PC1) females laid earlier (Figure 5), and there was a nonsignificant, but qualitatively similar, negative trend for the male's PC1 and laying date (Table 5).

Table 5
Relationships between laying date and male and female nonornamental and ornamental traits

	Simple effect				Age controlled			
	Estimate	t	df	p	Estimate	t	df	p
Males								
Tarsus	0.129	2.03	26	.053	0.150	2.42	25	.023[a]
Wing	−0.026	1.17	26	.252	−0.022	0.967	25	.343[a]
Mass	0.001	1.47	26	.152	0.023	2.36	25	.026[a]
Ornament PC1	−0.110	1.94	26	.063	−0.129	1.39	25	.178[a]
Ornament PC2	−0.062	1.23	26	.229	−0.060	1.21	25	.239[a]
Age	−0.130	1.31	26	.202	—	—	—	—
Females								
Tarsus	0.003	0.09	44	.928	−0.002	0.05	43	.964
Wing	0.020	1.15	44	.258	0.021	1.25	43	.217
Mass	−0.019	1.54	44	.130	−0.023	1.99	43	.053
Ornament PC1	−0.189	3.61	44	.001[b]	−0.187	2.31	43	.026[a]
Ornament PC2	−0.020	0.49	44	.626	−0.041	1.05	43	.299
Age	−0.302	2.51	44	.016[b]	—	—	—	—

[a] Indicates that if the term is forced into the model before age, then age has no significant effect.

[b] Significant differences at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis.

For polygynous males, only the primary female is included. Analysis is by linear regression on $\log_{10}$-transformed relative lay date. The left-hand columns of tests are simple regressions, and the right-hand columns refer to multiple regressions with age entered first.

However, as with clutch size, female age was related to laying date (Table 5). Female PC1 still showed a suggestive negative trend with lay date after controlling for female age ($p = .026$, ns after Bonferroni correction; Figure 5; Table 5), whilst the age relationship disappeared altogether in the same multiple regression ($t_{42} = 0.03$, $p = .975$). There were no differences in laying date between the primary females of polygynous males and monogamous females ($\log_{10}$-transformed laying date; $t_{23} = 0.06$, $p = .951$).

The proportion of time that parents were observed incubating was not related to ornamentation in either sex (males: PC1, $r_{16} = -.163$, $p = .519$; PC2, $r_{16} = .095$, $p = .707$; females: PC1, $r_{21} = .259$, $p = .233$; PC2, $r_{21} = -.415$, $p = .049$). The trend with female PC2 was not significant after sequential Bonferroni correction. Controlling for male incubation time when analyzing female relationships (using partial correlation) and vice versa for male relationships did not increase the strength of any correlations (e.g., female PC2: partial $r_{20} = -.397$, $p = .068$). Proportion of time incubating was not related to age in males ($b = -8.657$, $F_{1,16} = 2.70$, $p = .120$) or females ($b = 8.05$, $F_{1,21} = 1.82$, $p = .191$). It neither differed between the primary females of polygynous males and monogamous females ($t_{19} = 0.08$, $p = .941$) nor even between monogamous and polygynous males ($t_{19} = 0.41$, $p = .691$).

Although not significant after Bonferroni correction for all feeding-rate analyses, male feeding rate tended to be negatively correlated with PC1 (Kendall's $\tau_{17} = -0.366$, $p = .046$) but not with PC2 ($\tau_{17} = -.088$, $p = .632$). The relationship between feeding rate and male age was weaker but also negative ($\tau_{17} = -.320$, $p = .141$). Female feeding rates showed no such patterns (PC1, $\tau_{32} = 0.040$, $p = .745$; PC2, $\tau_{32} = 0.029$, $p = .816$; age: $\tau_{31} = 0.000$, $p = 1.000$). There were no differences in feeding rates between the primary females of polygynous males and monogamous females ($t_{16} = 0.021$, $p = .983$) or between monogamous and polygynous males ($t_{16} = 0.995$, $p = .334$).

The total number of fledglings produced, when both nests of polygynous males were pooled, tended to be positively related to male PC1 because more ornamented males were more likely to become polygynous (Figure 6). However, fledgling output was strongly related to the age of males and as

Table 6

Relationships between total fledging output and male and female nonornamental and ornamental traits

	Simple effect			Age controlled		
Parameter	Estimate	χ^2	p	Estimate	χ^2	p
Males						
Tarsus	0.160	2.16	.142	0.088	1.04	.309
Wing	0.010	0.07	.790	−0.002	0.00	.963
Mass	0.022	1.81	.179	0.004	0.10	.754
Ornament PC1	0.211	5.24	.022	−0.056	0.17	.677
Ornament PC2	−0.054	0.40	.526	−0.084	1.62	.203
Age	0.540	14.44	<.001[a]		—	—
Females						
Tarsus	−0.050	2.09	.149	−0.046	1.90	.168[b]
Wing	−0.008	0.22	.636	−0.011	0.40	.525[b]
Mass	−0.001	0.00	.956	−0.001	0.00[b]	.947
Ornament PC1	0.148	7.15	.008[a]	0.116	1.55	.212[b]
Ornament PC2	−0.105	6.55	.011[a]	−0.080	3.50	.061[b]
Age	0.144	5.56	.018	—	—	—

[a] Significant differences at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis.

[b] Indicates that if the term is forced into the model before age, then age also ceases to have a significant effect.

$n = 26$ for males, 46 for females. For polygynous males, both females were included. Analysis was by GLMs with Poisson error, and the scale parameter was adjusted to account for underdispersion. χ^2 Tests, with 1 df, are based on the change in log likelihoods as a result of adding the factor in question. The left-hand columns of tests are based on the change compared to a model with only a constant term. The right-hand columns of tests are the effect of the factor after controlling for age by forcing it into the model first.

Table 7

Relationships between percentage hatching success, percentage fledging success, and male and female nonornamental and ornamental traits

	Hatching success			Fledging success		
Parameter	Estimate	χ^2	p	Estimate	χ^2	p
Males						
Tarsus	−0.039	1.01	.315	0.010	0.04	.850
Wing	0.026	5.88	.015[a]	−0.001	0.00	.970
Mass	0.021	1.81	.179	0.002	0.10	.750
Ornament PC1	0.088	5.89	.015[a]	−0.056	0.96	.327
Ornament PC2	0.041	1.99	.159	−0.015	0.12	.724
Age	0.084	1.25	.263	0.072	0.45	.502
Females						
Tarsus	0.026	1.64	.200	−0.041	2.02	.155
Wing	0.014	2.10	.147	−0.023	2.34	.126
Mass	0.014	4.46	.035	−0.009	0.76	.384
Ornament PC1	0.121	11.92	<.001[a]	−0.000	0.000	.998
Ornament PC2	0.011	0.03	.615	−0.082	5.85	.016
Age	0.037	0.77	.380	0.032	0.27	.602

[a] Significant at a tablewide $\alpha = 0.05$, using sequential Bonferroni analysis.

$n = 26$ for males, 46 for females. For polygynous males, only the primary female is included. Analysis is by GLMs with Poisson error and log-link function. All hatching success models have clutch size as a covariate; all fledging success models have hatchling number as a covariate. χ^2 Tests, with 1 df, are based on the change in log likelihoods as a result of adding the factor in question.

above, the trend in relationship to PC1 disappeared after controlling for age (Table 6). The effect of male age on fledging output was not simply because older males were more likely to be polygynous. When both male age and mating status were entered into a GLM, only age remained significant (mating status: $\chi^2 = 1.60$, $p = .205$; age: $\chi^2 = 10.26$, $p = .001$). Fledgling output was significantly related to female ornamentation (PC1 and also, this time, PC2), but age was marginally nonsignificant after Bonferroni correction. That said, controlling for age rendered both PCs nonsignificant.

Fledgling output is a function of clutch size, hatching success, and survival from hatching to fledging, so the latter two components were analyzed separately. The number of hatchlings was, of course, strongly related to clutch size (parameter estimate = 0.488, $\chi^2 = 9.18$, $p = .003$), so clutch size was entered as a covariate in all analyses. The effects in Table 7 therefore represent effects on relative hatching success (i.e., relative to a given clutch size). Hatching success was strongly positively related to female PC1 ornamentation but not age (Table 7; forcing age into the model did not alter the significance of PC1). Hatching success was also significantly related to male PC1 and wing length (Table 7). The relationship with male PC1 disappears when female PC1 was forced into the model ($\chi^2 = 0.70$, $p = .404$), but a positive association with male wing length remains ($\chi^2 = 4.87$, $p = .027$). Therefore, any relationship with male ornamentation is an indirect effect of assortative pairing with ornamented females, but there is a small, independent correlation with male wing length. Fledging success relative to brood size (i.e., with number of hatchlings entered as a covariate; parameter estimate = 0.442, $\chi^2 = 19.72$, $p < .001$) was not significantly related to any male or female attributes.

The mass of nestlings close to fledging (age 18 days) was not strongly related to any ornamental variables or age of either parents but showed nonsignificant negative trends with male PC1 and age (males: PC1, $r_{24} = -.447$, $p = .025$; PC2, $r_{24} = -.274$, $p = .184$; age, $b = -4.623$, $F_{1,24} = 3.53$, $p = .073$; females: PC1, $r_{24} = -.266$, $p = .092$; PC2, $r_{24} = -.115$, $p = .475$; age, $b = -2.108$, $F_{1,24} = 2.17$, $p = .148$; none significant after Bonferroni correction). Forcing male age into a multiple regression of nestling mass on male PC1 removed the trend with the latter (PC1: $b = -3.015$, $F_{1,24} = 1.85$, $p = .187$) and vice versa (age: $b = -0.454$, $F_{1,24} = 0.01$, $p = .908$). There were no differences in nestling masses between the primary nests of polygynous males and those of monogamous females ($t_{21} = 1.02$, $p = .321$).

DISCUSSION

Ornaments as quality and age indicators

Many studies have provided evidence that ornaments are the product of sexual selection (Andersson, 1994). However, most studies have concentrated on male ornamentation, although the females of several species express the same ornament, usually to a smaller extent, as the males. Male and female European starlings possess similar throat feathers, even though there is clear sexual dimorphism once age has been accounted for (Feare, 1984; this study). These feathers are much more variable between individuals than nonornamental morphological traits, a pattern that is typical of ornamental traits in birds (e.g., Alatalo et al., 1988; Blanco and De la Puente, 2002; Grant et al., 1985; Jones and Montgomerie, 1992; Jones et al., 2000; Kraaijeveld et al., 2004) and that is consistent with these traits being the product of sexual selection (Andersson, 1994). Starlings are markedly sexually dimorphic with regard to PC1 of throat feather traits, consisting primarily of tip length, the iridescent portion, and hue index. PC1 scores were higher for males than females and

higher for older birds, but there is no sex-by-age interaction, and inspection of PC1 indicates that sex and age variation fall along the same axis (Figure 3). PC2, consisting of the chromatic index and the brightness index, was similar for all birds regardless of sex or age. Although old females and young males had similar PC1 scores, this is not to say that they are indistinguishable: the sexes differ in bill-base coloration, the presence of a light ring in the eye of females, and behaviors such as song (Feare, 1984).

We argue that male and female throat feather ornaments (viz. PC1 characteristics) in starlings are age and/or quality indicators and could be the product of mutual sexual selection. Leaving aside, for the moment, whether quality or age is being assessed through throat feather characteristics or via some other cue (such as song output or song complexity; Eens et al., 1991), we have evidence of fitness benefits to older more ornamented individuals in both sexes. However, it is notable that males and females did not gain fitness advantages in the same way.

The benefits to a male of mating with an older ornamented female seem obvious and are direct fitness gains. Older, more ornamented females bred earlier and laid larger clutches. After controlling for the effect of age or ornamentation of the pair male, the ornamentation and age of the pair female remained significantly positively associated with lay date and clutch size. The timing of breeding in starlings is important because it affects the first year survival of young, with first year survival decreasing as the season progresses (Karlsson, 1983; Smith et al., 1994). A similar phenomenon occurs in Inca terns (*Larosterna inca*; Velando et al., 2001) and in great cormorants (*Phalacrocorax carbo*; Childress and Bennun, 2002), in which more intensely ornamented pairs bred earlier and had higher fledging success. Therefore, even though more ornamented females were not "better parents" (there was no relation between female ornamentation or age and incubation or feeding), a male mated to an older more ornamented female benefited because she laid early, large clutches that also hatched more successfully after controlling for clutch-size differences. More ornamented, older, females therefore fledged more young in total.

Older (more ornamented) males seem to be more attractive to females—at least in that they were more likely to become polygynous—but even the mates of monogamous males and the primary females of polygynous males enjoyed no obvious direct benefits from pairing with older more ornamented partners. If anything, there were costs, as such males tended to feed the nestlings less. The positive relations between male ornamentation and fitness correlates such as lay date, clutch size, and relative hatching success were only by virtue of the fact they were paired with older more ornamented females.

There was no relationship between ornamentation and body mass in either sex, but the earlier lay date and higher clutch size of more ornamented females suggest that female ornamentation and condition at laying were likely to have been correlated. Our birds were weighed by the time the nestlings had hatched, when energy stores had been used for reproduction, with more ornamented females spending more energy on egg production. Such a pattern has been shown in bluethroats (*Luscinia svecica svecica*), with a positive association between female ornamentation and body mass during the prebreeding period but no association during the nestling stage (Rhode et al., 1999). Whatever the situation in starlings, female ornamentation potentially provides information on female reproductive capacity, although the data presented in this paper do not constitute proof that they do function as such a signal. For the PC1 throat feather characteristics to fulfill the requirements of honest advertisement models (Grafen, 1990; Kodric-Brown and Brown, 1984), there must be differential costs of ornament expression with respect to quality (Grafen, 1990; Pomianowksi et al., 1991). The costs of developing and maintaining carotenoid-based coloration are well researched (e.g., Hill, 2002; Olson and Owens, 1998), but structural colors have received little attention. The main costs considered for plumage coloration in the literature are social, predation risk, direct energetic or nutrient limitation, and hormone mediated. There is little evidence for a substantial social cost of maintaining throat feather characteristics in starlings. Dominants do not seem to regularly test subordinates on the honesty of their signals, and during the 3 years of study we have never witnessed escalated fights resulting in serious injury in the loser. Predation risk seems unlikely as the iridescence of starling feathers is only apparent when (very) close-up; at a distance starlings are dark birds. Direct or hormone-mediated developmental costs seem more likely and are important avenues for future research. It has been suggested that precise deposition of the keratin and melanin layers that create iridescent colors may be physiologically "difficult" (Andersson, 1999). There is some evidence for individual quality-related differences in producing noniridescent structural colors (Keyser and Hill, 1999, 2000), but no comparable research on iridescent plumage has been carried out. A hormone-mediated mechanism of honest signaling, such as an immunocompetence handicap, may seem unlikely because starlings develop breeding plumage when the gonads are fully regressed and testosterone levels are low (Feare, 1984). However, the same is true of the melanin-based chest bib of sparrows, *Passer domesticus*, and here testosterone is central to the proximate control of the trade-off between benefits and costs of ornament expression (Buchanan et al., 2001; Evans et al., 2000).

Age or ornamentation?

In our starlings the PC1 throat feather traits, but not the PC2 throat feather traits, were highly correlated with age. The strength of the correlation makes it hard in most, but not all, cases to separate statistically the relative influences of age and ornamentation on other variables. Several other studies have found that ornaments are age dependent (e.g., Grant BR and Grant PR, 1987; Sundberg and Larsson, 1994). The age-related changes we have described are not delayed loss of juvenile plumage. Juvenile starlings have a distinct, noniridescent plumage that is molted in their first winter (Feare, 1984). Nevertheless, many of the relationships between PC1 ornamentation and other variables may be explained by differences in age. It could be advantageous for an individual to choose an older mate in that it proves it to have good viability, which may be heritable, and probably more experience. For either sex, age indicates that you have survived (so providing possible good-genes benefits) and have experience as a parent. For females, older males may have better knowledge of good nesting sites or can defend them better. For males, older females offer fecundity advantages, which is clear in our study and quite widespread as a phenomenon in other birds (reviewed by Newton, 1989). Bearing this in mind, it is possible that PC1 ornamentation is not a signal, is not assessed, and any relationships we observe are an incidental by-product of some other age-related cue. The assortative pairing by PC1 that we observed was no longer evident when we controlled for age-assortative pairing (although the converse was also true; age-assortative pairing was no longer evident when we controlled for PC1-assortative pairing). We can rule out mate fidelity as a passive explanation of age-assortative pairing; all pairs were newly formed in the year of study. However, male song complexity, which is correlated with age (Eens et al.,

1991), is preferred by female starlings (Gentner and Hulse, 2000; Mountjoy and Lemon, 1996). The evidence against this being a complete explanation of our results is that we know that the reflectance spectra of male throat feathers affect female choice (Bennett et al., 1997; Maddocks et al., 2002). Therefore, it is possible that PC1 ornamentation, which is an excellent predictor of age, is a signal, like song complexity, that starlings use to select older mates. We cannot conclude that there is any information content in the throat feathers (e.g., about mate quality) above and beyond the information on age. However, age may be the main determinant of variation in the qualities sought in a starling mate by either sex, given the proximate benefits of mating with an older (ornamented) partner.

The statistical inseparability of ornamentation and age in relation to mate quality, as elucidated in this study, gives a warning about interpretations of studies showing correlates of ornamentation with quality when age information is unavailable. However, if the qualities sought in a mate vary with age, then controlling for age in an analysis of ornamentation may remove the major source of variation in both the quality measures and the ornamentation that signals these qualities to a mate. This would result in a lack of correlation between quality measures and ornamentation, when controlling for age statistically, even though the ornamentation is signaling these qualities. The goals of future research should be to establish the relevance of signaling age and how age can be signaled reliably.

Mutual sexual selection through mutual mate choice?

Mate choice, competition over mates, and competition over resources are not mutually exclusive processes, and their effects are likely to be additive (West-Eberhard, 1983). The ability to defend resources necessary for successful breeding have a positive effect on offspring survival and therefore on fitness of both members of the pair. Breeding adults thus gain fitness benefits in the form of increased reproductive success from pairing with a high-quality partner. In starlings, there is a positive association between PC1 throat feather characteristics and correlates of fitness in males and females; birds with higher PC1 scores bred earlier in the season, and produced larger clutches and more fledglings. However, for ornamentation to have an effect on mutual sexual selection driven by mate choice, it needs to have an effect on the fitness of individuals of both sexes (Tanaka, 1996). In starlings, females are known to select males based on song (Eens et al., 1991, 1993) and preferences are affected by throat feather coloration (Bennett et al., 1997; Maddocks et al., 2002), and females in our study population had the opportunity to choose among mates. All females became mated, and a large fraction of males remained unmated throughout the breeding season (Brouwer and Komdeur, 2004). Our study showed that starlings of either sex do not gain obvious "good parent" benefits of mating with partners with well-developed feather characteristics. Females and males do not gain increased incubation and nestling provisioning when mated with highly ornamented partners. Indeed, the reverse appears to be true: more ornamented males tended to feed nestlings less. Among the species studied so far, there are only three others in which the relation between female provisioning and female ornamentation has been investigated. In barn swallows (*Hirundo rustica*, Cuervo et al., 1996) and bluethroats (Rhode et al., 1999) there was no correlation between ornamentation and provisioning rate, whereas in Northern cardinals (*Cardinalis cardinalis*; Linville et al., 1998) there was a positive correlation. We suggest that direct reproductive benefits for males, and indirect genetic benefits for females (or maybe both sexes), play an important role in mate choice based on throat feather characteristics. Males mated with older females with high PC1 scores had larger clutches and produced more fledglings. In multiple regressions, where age was entered as well as PC1, the relationships of clutch size or laying date and female PC1 remained stronger than the relationships with female age (although our conservatism in use of Bonferroni correction rendered relationships with PC1 nonsignificant). This suggests that female PC1 may signal aspects of quality beyond those attributable to age, but only further study can settle this point. The benefits to females in choosing older, more ornamented males are elusive; there were no direct benefits detectable in our study (only costs), and the establishment of possible genetic benefits awaits further data.

Sexual dimorphism of ornamentation

The sexual dimorphism of male and female throat feather ornaments must be explained by a different balance point in males and females between the sexually selected benefits of displaying the ornaments and the energetic and social costs of producing and maintaining them. This sexual dimorphism could be related to the following factors: (1) higher mating success benefits of ornament expression to males. In starlings, it is mainly the male that is active in social competition over resources necessary for breeding. Polygynous males are dominant over monogamous males in the acquisition of nest-boxes (Komdeur, Brouwer L, personal observation), which may be an age effect, given the correlation between mating status and age. Older male starlings (with high PC1 scores) had a higher chance of becoming polygynous. Given that age and ornamentation are correlated, the outcome of conflicts may depend on the intensity of ornamentation. However, other studies have failed to find a relation between competitive ability and ornament expression. In moorhens (Petrie, 1984, 1988), crested auklets (Jones and Hunter, 1999), and black swans (Kraaijeveld et al., 2004), both sexes use ornaments as an indicator of dominance, but males are more often the aggressive sex. (2) Differences between males and females in ability to produce or bear the ornament. The classic argument of Wallace (1889) that sex differences in plumage are the result of selection against conspicuousness in nesting females needs consideration but seems less plausible in a hole-nesting species that, from a distance, is dark-colored (see above). Future investigation of differences in mating behavior, exploring the possibility of increased variation in both sexes' mating success via extrapair copulations and egg dumping, and the costs of ornament expression should shed light on this question.

In conclusion, our results suggest that throat feather ornaments could be favored by mutual sexual selection and may have a signaling function in both sexes of the European starling. These feathers provide reliable information on age and, perhaps as a result or perhaps in addition, individual quality. However, we do not know if that information is actually used; other cues could be more important. Furthermore, the proximate benefits of mating with an older ornamented partner appear to differ between the sexes. Our tentative conclusion sets the stage for several interesting hypotheses to be tested in future manipulative experiments. Experimental studies are required to test the proximate factors involved in throat feather development and maintenance, how the different throat feather characteristics relate to quality, and whether coloration and feather length affect preferences in the same way in both sexes. To unravel the role of age and throat feather ornamentation as indicators of mate quality, future work must be done to establish whether there is a significant variation in the fitness benefits of mate choice within age

categories and whether feather attributes provide reliable information in this regard.

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